Effects of land-use patterns on soil microbial diversity and composition in the Loess Plateau, China

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Abstract: In the Loess Plateau of China, land-use pattern is a major factor in controlling underlying biological processes. Additionally, the process of land-use pattern was accompanied by abandoned lands, potentially impacting soil microbe. However, limited researches were conducted to study the impacts of land-use patterns on the diversity and community of soil microorganisms in this area. The study aimed to investigate soil microbial community diversity and composition using high-throughput deoxyribonucleic acid (DNA) sequencing under different land-use patterns (apricot tree land, apple tree land, peach tree land, corn land, and abandoned land). The results showed a substantial difference ($P<0.050$) in bacterial alpha-diversity and beta-diversity between abandoned land and other land-use patterns, with the exception of Shannon index. While fungal beta-diversity was not considerably impacted by land-use patterns, fungal alpha-diversity indices varied significantly. The relative abundance of Actinobacteriota (34.90%), Proteobacteria (20.65%), and Ascomycota (77.42%) varied in soils with different land-use patterns. Soil pH exerted a dominant impact on the soil bacterial communities' composition, whereas soil available phosphorus was the main factor shaping the soil fungal communities' composition. These findings suggest that variations in land-use pattern had resulted in changes to soil properties, subsequently impacting diversity and structure of microbial community in the Loess Plateau. Given the strong interdependence between soil and its microbiota, it is imperative to reclaim abandoned lands to maintain soil fertility and sustain its function, which will have significant ecological service implications, particularly with regards to soil conservation in ecologically vulnerable areas.

Keywords: abandoned lands; land-use pattern; soil property; diversity of soil microbe; soil microbial community

1 Introduction

The microbiome, characterized by its high abundance, diversity, and metabolic activity, constitutes a pivotal element in soil ecosystems. It plays an essential role in governing ecological processes and biogeochemical cycling, particularly organic decomposition (Tedersoo et al., 2014; Yang et al., 2020a; Yang et al., 2022). The microbial communities are highly sensitivity to environmental changes, particularly those resulting from anthropogenic land-use alterations (Xu et al., 2021; Zhang et al., 2022; Dou et al., 2023; Mishra et al., 2023). Land-use changes induce shifts in plant communities and soil conditions, leading to changes in the quantity, quality, spatial distribution, and temporal availability of microbial substrates. Consequently, these changes subsequently impact the diversity and composition of microbial communities (Liu et al., 2022;

Yang et al., 2023; Zhang et al., 2023). For instance, Sawada et al. (2021) found that the conversion of mixed natural forest land to a cedar plantation resulted in an increase in bacterial diversity, but a decrease in specific bacteria that promote plant growth and ectomycorrhizal fungi. Xu et al. (2021, 2023) found that soil microbial community composition assembly and co-occurrence patterns were more susceptible to land-use types and their duration in the farming-pastoral ecotone, particularly during conversions between cropland and grassland. The changes in soil microbial communities could further elicit responses in soil function under land-use changes due to their pivotal roles in regulating nutrient stocks and transformations (Yang et al., 2023). Unfortunately, our understanding of the impacts of these land-use changes remains limited. Therefore, gaining a comprehensive understanding of the potential impact of land-use changes on soil microbial community composition and diversity offers valuable insights into the response mechanisms governing the structural and functional stability of terrestrial ecosystems in relation to such changes.

The Loess Plateau of China is among the most severely eroded areas globally, primarily due to the combined effects of population pressure and environmental degradation (Feng et al., 2016; Feng et al., 2017; Yang et al., 2020b). The Loess Plateau, renowned as one of the most fragile ecosystems in China, is characterized by extensive distribution of loess, severe soil erosion, desertification, and low vegetation coverage (Xu et al., 2019; Wu et al., 2023). The Grain-for-Green Project aims to safeguard and enhance the ecological environment, with a specific focus on soil and water conservation (Deng et al., 2014; Fu et al., 2017). Meanwhile, to increase economic income, large areas of cultivated land have been converted to economic forest land or changed their crop planting patterns, leading to significant land-use changes in this area. Related studies have shown that conversion of cultivated land to forest land leads to an increase in soil bacterial diversity, mainly associated with an increase in the phylum Proteobacteria in the Loess Plateau. Soil available phosphorus, available potassium, and vegetation biomass were the key factors affecting bacterial communities in land-use conversion (Zhang and Lv, 2021). While Yang et al. (2020a) found that soil microbial diversity exhibited significant associations not only with vegetation type, but also with soil pH and soil organic carbon (SOC) during vegetation restoration in the Loess Plateau. Furthermore, the abandonment of cultivated land has been steadily increasing as a result of a significant outflow of labor forces in recent years (Zhang et al., 2023). Cultivated land abandonment leads to a significant reduction in soil fungal diversity, significantly altering the relative abundance at the bacterial phylum level (Zhang et al., 2023). However, due to the intricate relationship between soil microbial communities and soil properties under different land-use patterns in the Loess Plateau, factors influencing soil microbial communities remain largely unclarified. Therefore, it is imperative to further advance research on the response of soil microbial communities and the underlying driving factors to land-use changes.

Accordingly, the objective of this study was to examine whether the conversion of land-use patterns in the Loess Plateau has impacted the diversity and composition of soil bacterial and fungal communities, as well as to identify the primary factors that influence these communities. We hypothesized that: (1) land-use patterns would elicit alterations in the diversity of soil microbial communities; (2) distinct land-use patterns would exhibit dissimilarities in soil microbial composition; and (3) soil pH and nutrients may be the main factors affecting the composition of soil bacterial and fungal communities across different land-use patterns.

2 Material and methods

2.1 Study area

This study was carried out in southern Lanzhou City, northwestern China (36°07′–39°09′N, 103°39′–103°41′E; 1550–1700 m a.s.l.; Fig. 1), which has continental semi-arid climate. The area experiences a mean annual precipitation of 250–360 mm, primarily concentrated in summer, with

an annual average temperature ranging from 5°C to 9°C. Additionally, the mean annual evaporation is 1650 mm and the frost-free period lasts for approximately 190 d. The native vegetation is composed of perennial clumped low grasses, xerophytic shrubs, and small semi-shrubs. The main soil types are calcareous soils. Cultivated land has been converted into economic forest land (orchards) since 2010, but a large amount of abandoned land has been maintained.

Fig. 1 (a), location of the sampling sites; (b), AL (abandoned land); (c), AT (apple land); (d), ATL (apricot land); (e), CL (corn land); (f), PTL (peach land). The abbreviations are the same as in the following figures. Note that the figure 1a is based on the standard map of the Earth Online (https://www.earthol.com/bd/), and the standard map has not been modified.

2.2 Field sampling and soil analysis

The study selected five land-use patterns in July 2020, which included planted economic forest land (orchards) and non-forest land. These land-use patterns comprised of apricot land (ATL), corn land (CL), apple land (AT), peach land (PTL), and abandoned land (AL) (Fig. 1). They were all converted and abandoned by cultivated land (wheat-potato rotation) in 2014, and these lands were located on terraces with an average slope of 30° and an easterly aspect. These lands, excluding AL, are fertilized with urea and diammonium phosphate at a rate of 225 kg/hm^2. Irrigation is applied at a rate of 285 m^3/ hm^2, three times per year. Since no adjacent land-use pattern was found in the area

with approximate slope and aspect, only one study site was selected. The plots within each land-use pattern were divided into five 10 m×10 m subplots. Within each subplot, three topsoil samples (0–10 cm depth) were collected along the diagonal line using a 50-mm diameter soil drill and combined to create a composite sample. A total of 25 soil samples were obtained. Meanwhile, cut rings (100 cm^3) were utilized to collect the complete soil core, which were subsequently dried at 105°C and weighed for determining of soil bulk density (BD).

Soil samples were partitioned into two parts, with one part being used to measure the physical and chemical properties of the soil. Soil samples were subjected to air-drying, crushing, and sieving through the 10- and 100-mesh sieves. Soil water content (SWC) was determined by oven-drying soil samples at 105°C until a constant mass (Li et al., 2021). Soil pH was measured using a standard pH meter with 2.5:1.0 water soil ratio (Widdig et al., 2020). Soil salt (SS) was determined in a soil and distilled water solution using a conductivity meter (FE38, Mettler Toledo International Inc., Greifensee, Switzerland). SOC was quantified through the wet dichromate oxidation method, followed by titration with $FeSO_4$ (Nelson and Carlson, 2012). Total nitrogen (TN) was conducted using the Kjeldahl method (Rutherford et al., 2007), while soil total phosphorus (TP) and available phosphorus (AP) were analyzed by ammonium molybdate method after persulfate oxidation (Zhang et al., 2023). Soil ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) were quantified by employing a SmartChen 200 element analyzer (AMS Corporation, Rome, Italy). About 2 g soil sample was extracted, and after eliminating impurities such as small stones and plant residues, it was subjected to deoxyribonucleic acid (DNA) sequencing for soil bacterial and fungi using dry ice incubation by Majorbio Bio-Pharm Technology Co., Ltd., Shanghai, China. Soil properties of the five land-use patterns are presented in Table 1.

Table 1 Soil properties among different land-use patterns

Soil property	AT	PTL	ATL	CL	AL
SOC (g/kg)	7.13±0.60[a]	7.58±1.57[a]	5.67±0.35[a]	7.34±1.10[a]	6.48±1.53[a]
TN (g/kg)	0.24±0.14[b]	0.56±0.10[a]	0.25±0.04[b]	0.36±0.04[ab]	0.18±0.04[b]
TP (g/kg)	0.63±0.13[ab]	0.31±0.08[b]	0.99±0.41[a]	0.19±0.07[b]	0.40±0.07[b]
NH_4^+-N (mg/kg)	2.81±0.37[ab]	2.69±0.44[ab]	4.16±0.88[a]	3.26±0.50[ab]	2.27±0.38[b]
NO_3^--N (mg/kg)	28.24±3.18[ab]	23.43±4.52[bc]	11.06±1.24[d]	33.76±2.76[a]	18.54±2.88[cd]
AP (mg/kg)	9.37±0.93[bc]	11.79±1.70[ab]	14.06±1.00[a]	8.97±1.27[bc]	7.03±0.63[c]
pH	8.47±0.04[a]	8.45±0.03[ab]	8.28±0.12[b]	8.41±0.03[ab]	8.55±0.03[a]
SS (g/kg)	0.06±0.002[a]	0.06±0.003[a]	0.09±0.03[a]	0.07±0.01[a]	0.05±0.01[a]
SWC (%)	0.48±0.32[a]	0.16±0.01[a]	0.13±0.01[a]	0.19±0.01[a]	0.15±0.04[a]
BD (g/cm^3)	1.73±0.03[a]	1.67±0.01[ab]	1.72±0.06[a]	1.65±0.03[ab]	1.57±0.08[b]

Note: Different lowercase letters within the same variable indicate significant differences among different land-use patterns at $P<0.050$ level. SOC, soil organic content; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus; SS, soil salinity; SWC, soil water content; BD, bulk density; AT, apple land; PTL, pear land; ATL, apricot land; CL, corn land; AL, abandoned land. The abbreviations are the same in the following tables. Mean±SE; n=25.

2.3 DNA extraction and polymerase chain reaction (PCR) amplification

The genomic DNA of the microbial community was extracted from soil samples using the Soil DNA Kit (Omega Bio-tek, Norcross, USA) following the manufacturer's instructions. Subsequently, the quality of the DNA extract was assessed by a 1% agarose gel and its quantification and purity were determined using a NanoDrop® 2000 UV-vis spectrophotometer (Thermo Scientific, Wilmington, USA). The internal transcribed spacer (ITS) sequence of the fungal 18S ribosomal ribonucleic acid (rRNA) gene was amplified using primers ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2R (5′-GCTGCGTTCTTCATCGATGC-3′). In addition, the hypervariable region V3-V4 of the bacterial 16S rRNA gene was amplified with primer pairs 338F (5′-ACTCCTACGGGAGG CAGCAG-3′) and 806R

(5′-GGACTACHVGGGTWTCTAAT-3′), employing an Applied Biosystems (ABI) GeneAmp® 9700 PCR thermocycler (ABI, Foster City, USA). The amplification of the 16S rRNA gene was performed using PCR under the following conditions: initial denaturation at 95°C for 3 min, followed by 27 cycles of denaturation at 95°C for 30 s, annealing at 55°C for 30 s, extension at 72°C for 45 s, and a final single extension step at 72°C for 10 min. The reaction was then terminated at 4°C. PCR mixtures consisted of the following components: TransStart FastPfu buffer (4.0 μL), deoxynucleotide triphosphates (dNTPs) (2.0 μL), forward primer (0.8 μL), reverse primer (0.8 μL), TransStart FastPfu DNA Polymerase (0.4 μL), template DNA (10 ng), and ddH$_2$O up to a total volume of 20.0 μL. All PCR reactions were performed in triplicates. PCR product was extracted from a 2% agarose gel and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, USA). Subsequently, the purified product was quantified using the QuantusTM Fluorometer (Promega Corporation, Madison, USA).

2.4   Illumina MiSeq sequencing

The purified amplicons were pooled equally and subsequently subjected to paired-end sequencing on an Illumina MiSeq platform (Illumina, San Diego, USA), following the standardized protocols provided by Majorbio Bio-Pharm Technology Co., Ltd., Shanghai, China.

2.5   Data analysis

Following data homoscedasticity and normality tests, a one-way analysis of variance (ANOVA) was performed to compare soil properties between various land-use patterns. A least significant difference post hoc test at $P<0.050$ level was then performed using SPSS v.22.0 software (SPSS Inc., Chicago, USA). The Uparse v.7.1 was utilized for clustering the initial sequences obtained from the soil samples (Edgar, 2013), eliminating singleton sequences without duplicates, and identifying sequence chimeras. Subsequently, we grouped the optimized sequences into operational taxonomic units (OTUs) based on varying levels of similarity using a sequence similarity threshold of 97% (equivalent to a distance limit of 3%). The coverage of the intact soil microbiome by the obtained sequences was confirmed through rarefaction analysis of the filtered OTUs using quantitative insights into microbial ecology (QIIME) v.1.8.

Alpha-diversity indices, including Chao1, Good's coverage, Shannon, and Sobs, were calculated using Mothur v.1.30.1. Using a Bray-Curtis dissimilarity matrix across different land-use patterns, we used non-metric multidimensional scaling (NMDS) analysis to evaluate the beta-diversity of microbial community structures in soil samples. To investigate the differences in soil microbial communities among experimental treatments, we performed a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations and employed the Bray-Curtis distance measure. To find statistically significant differences in abundance, we applied the non-parametric Kruskal-Wallis (KW) sum-rank test, and detected groups displaying a significant difference. A Venn diagram was employed to compare the similarity and dissimilarity among bacterial and fungal communities across different land-use patterns, depicting shared and unique OTUs. LEfSe was utilized to perform linear discriminant analysis (LDA) and to identify taxonomic soil bacterial or fungal taxa that exhibit significant relative abundance differences among various land-use patterns. Additionally, using R v.3.6.2 (package vegan), we carried out redundancy analysis (RDA) and Spearman correlation analysis to evaluate the association between soil characteristics and dominant bacterial and fungal phyla across various land-use patterns.

3   Results

3.1   Alpha- and beta-diversity of soil microbial community

A total of 3,401,204 high-quality bacterial sequences and 3,262,059 fungal sequences were identified across all land-use patterns. Using 97% sequence similarity criteria, we further divided these sequences into 9218 bacterial and 3501 fungal OTUs. The bacteria were from 38 phyla, 128 classes, 329 orders, 520 families, and 969 genera. The fungi were from 14 phyla, 44 classes, 118

orders, 185 families, and 671 genera. High Good's coverage of bacteria and fungi (96.11%–99.88%) indicates that the sequencing depth achieved sufficient coverage of most microorganisms, including some rare species.

For soil bacteria, Shannon index did not exhibit any significant variation among different land-use patterns, whereas a notable disparity was observed in Sobs index, Good's coverage, and Chao1 index (Table 2). While Sobs and Chao1 in AL were much lower than those of other land-use patterns, Good's coverage of bacterial species in AL was significantly larger than those of other land-use patterns (Table 2). For soil fungi, alpha-diversity indices exhibited significant variations across various land-use patterns (Table 2). Chao1 and Sobs indices of AL were significantly lower than that of AT, and Good's coverage of AL was significantly higher than that of AT. Shannon index of AT was much greater than that of ATL, while Chao1 and Sobs indices of AT were significantly higher than those of other land-use patterns. Compared with AT, ATL, and AL, Good's coverage of PTL was noticeably greater (Table 2).

Table 2 Differences in microbial diversity among different land-use patterns

Microbe	Land-use pattern	Good's coverage (%)	Chao1	Shannon	Sobs
Bacteria	AT	0.9612[b]	4091.90±58.99[a]	6.6763±0.02[a]	2857.80±43.07[a]
	PTL	0.9623[b]	3982.55±137.66[a]	6.6276±0.05[a]	2852.20±81.26[a]
	ATL	0.9626[b]	3906.05±100.82[a]	6.5571±0.07[a]	2755.40±83.67[a]
	CL	0.9636[b]	3898.12±94.33[a]	6.6394±0.01[a]	2753.00±34.95[a]
	AL	0.9691[a]	3311.57±257.73[b]	6.4621±0.14[a]	2427.60±170.74[b]
Fungi	AT	0.9979[b]	500.38±14.10[a]	4.3488±0.13[a]	442.80±15.69[a]
	PTL	0.9988[a]	371.67±30.87[b]	3.8334±0.28[ab]	349.40±28.77[b]
	ATL	0.9980[b]	415.26±26.32[b]	3.4909±0.31[b]	365.80±26.67[b]
	CL	0.9979[b]	414.17±28.91[b]	3.5820±0.41[ab]	355.20±28.91[b]
	AL	0.9988[a]	365.56±28.63[b]	3.9021±0.23[ab]	336.20±25.52[b]

Note: Different lowercase letters within the same microbe indicate significant differences under different land-use patterns at $P<0.050$ level. Mean±SE.

This study demonstrated variations in the bacterial and fungal community composition of soil depending on NMDS for various land-use patterns. The results indicated substantial differences in soil bacterial community composition between AL and other land-use patterns ($P=0.001$; Fig. 2a), whereas no significant differences were identified in soil fungal community composition among different land-use patterns ($P=0.071$; Fig. 2b). Furthermore, the stress values indicated that the results were well interpretable.
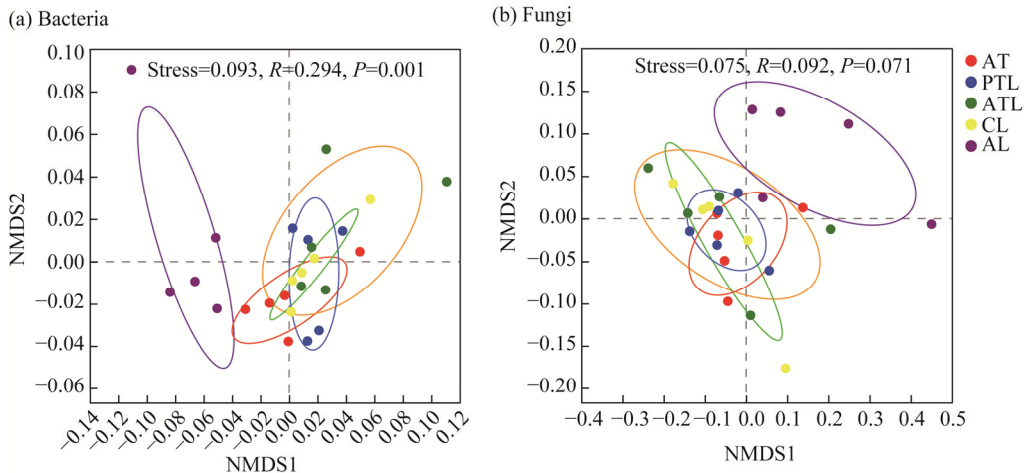

Fig. 2 Non-metric multidimensional scaling (NMDS) analysis of bacteria (a) and fungi (b) among different land-use patterns at the phylum level. R value is the ANOSIM (analysis of similarities) statistic R, and P value is the significance from permutation.

3.2 Taxonomic distribution of microbial community

Taxonomic distribution of microbial community under different land-use patterns is shown in Figure 3. The Actinobacteriota phylum dominated the bacterial community across all land-use patterns, comprising 34.90% of the total sequence. It was followed by Proteobacteria (20.65%), Chloroflexi (15.43%), Acidobacteriota (12.56%), Gemmatimonadota (3.87%), Bacteroidota (2.28%), Myxococcota (2.02%) and Firmicutes (1.72%) (Fig. 3a and c). In AL, Actinobacteriota exhibited a significantly higher relative abundance compared with other land-use patterns, while the Proteobacteria displayed a significantly lower relative abundance than those found in other land-use patterns except AT. Chloroflexi displayed a significantly higher relative abundance in AT than in ATL. The relative abundance of Firmicutes was significantly higher in PTL than in AL. There were no significant differences in the abundances of Acidobacteriota, Myxococcota, and Cyanobacteria among the five land-use patterns.

Ascomycota was the most dominant phylum in fungal communities across all land-use patterns, accounting for 77.42% of total sequences, followed by Basidiomycota (10.58%), Mortierellomycota (7.64%), Unclassified_k_Fungi (3.14%), Chytridiomycota (0.76%) and Glomeromycota (0.32%) (Fig. 3b and d). No significant difference was observed in the relative abundance of Ascomycota, Basidiomycota, Mortierellomycota and Chytridiomycota. However, the relative abundance of Unclassified_k_Fungi in AL was significantly higher than those of other land-use patterns (Fig. 3d).

The number of OTUs shared by the bacterial communities of the five land-use patterns was 2551. In terms of unique OTUs, AL had the highest number of unique OTUs, numbered 560. The least number of unique OTUs was found in AT and CL, numbered 251 (Fig. 4a). The fungal
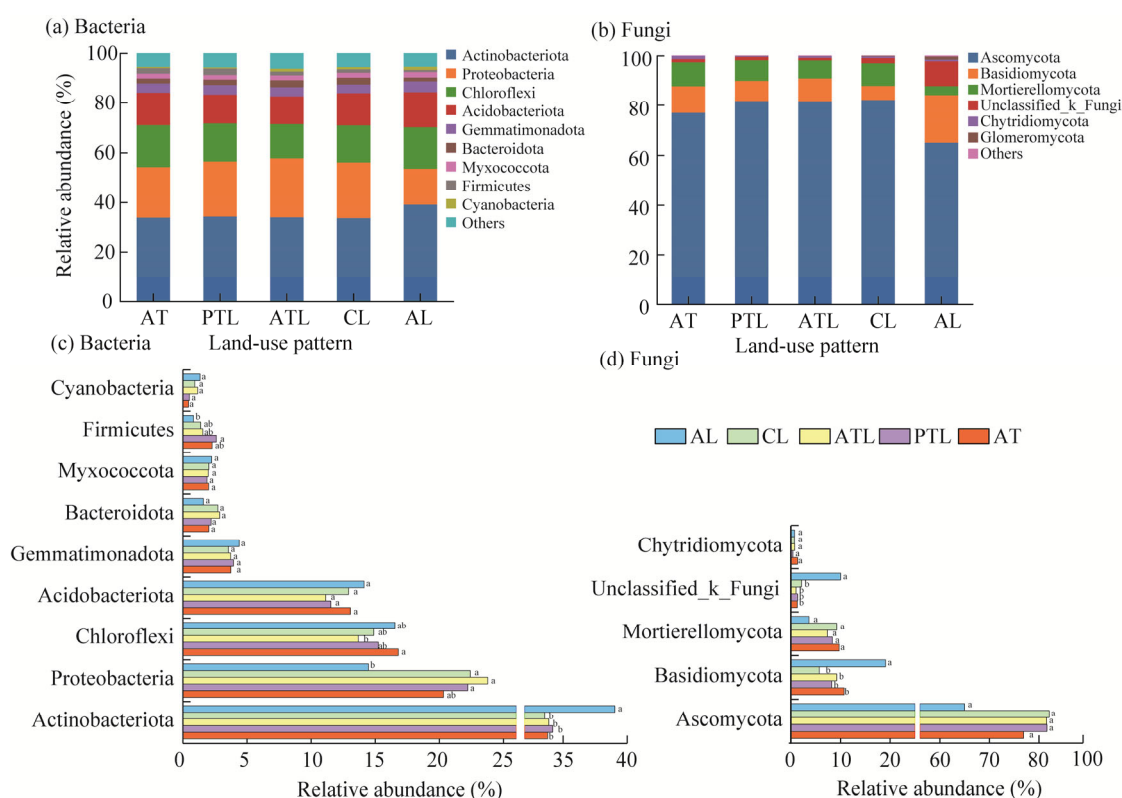

Fig. 3 Relative abundance of dominant bacterial (a and c) and fungal (b and d) communities at the phylum level among different land-use patterns. Different lowercase letters within the same microbe indicate significant differences under different land-use patterns at $P<0.050$ level.
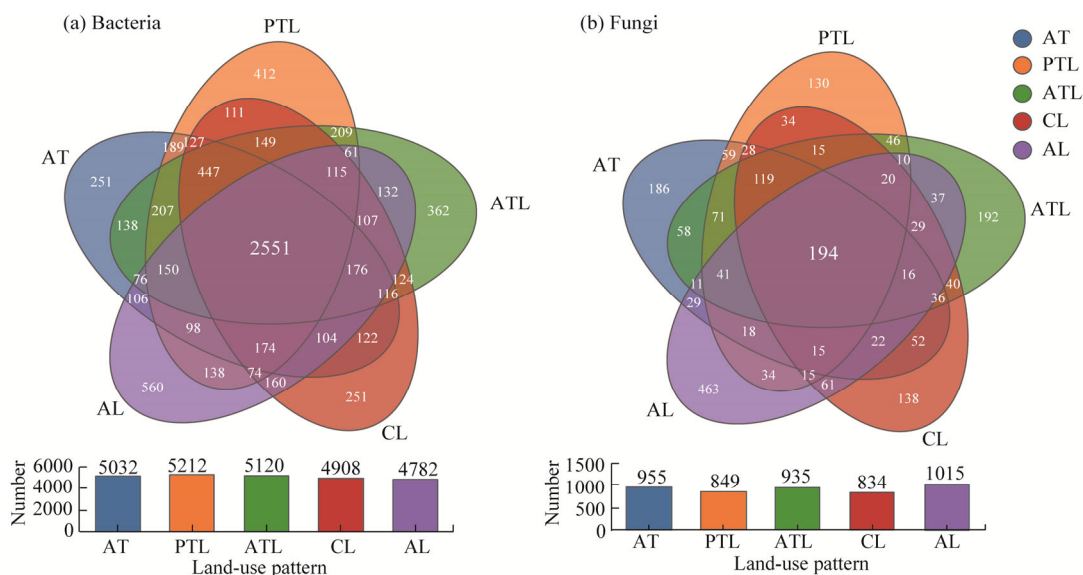
Fig. 4 Venn diagram represents the operational taxonomic units (OUTs) of bacterial (a) and fungal (b) communities among different land-use patterns

community in five land-use patterns shared a total of 194 OTUs. AL had the highest number (463) of unique OTUs, while PTL had the lowest number (130) (Fig. 4b).

The LEfSe analysis was performed to identify bacterial taxa that exhibited significant differences in relative abundance among soil samples. As depicted in Figure 5, a total of 20 bacterial clades (1 in AT, 5 in PTL, 4 in ATL, and 10 in AL) and 38 fungal clades (12 in AT, 6 in PTL, 6 in ATL, 7 in CL, and 7 in AL) showed statistically significant differences across all soil samples with an LDA threshold of 4.0. The bacterial biomarkers at the phylum level were found to be associated with Actinobacteriota, Proteobacteria, and Chloroflexi, while the fungal biomarkers were affiliated with Unclassified_k_Fungi. Among these groups, Proteobacteria was found to be dominant in ATL, Chloroflexi in AT, and Actinobacteriota in AL. Additionally, Unclassified_k_Fungi was identified as the dominant species in AL.

3.3   Relationship between soil property and soil microbial community

For soil bacteria, RDA revealed that the first and second ordination axes accounted for 49.69% and 14.46% of the variance in total phylum among different land-use patterns, respectively. The pH and AP were identified as the primary factors influencing the composition of bacterial communities (Fig. 6a; Table 3). Regarding fungi, RDA indicated eigenvalues of 47.91% and 3.49% for the first and second axes, respectively, with AP being identified as the primary factor affecting fungal community composition (Fig. 6b; Table 3).

Spearman correlation coefficient revealed a significant positive association between pH and Acidobacteriota as well as Chloroflexi in soil bacteria, while the result showed a significant negative relationship of pH with Proteobacteria and Bacteroidota. There was a strong negative link between SS and Myxococcota, and a significant positive correlation between SS and Bacteroidota. AP exhibited a significant positive correlation with Proteobacteria. Additionally, it was shown that NO_3^--N correlated positively with Cyanobacteria, but negatively with Actinobacteria (Fig. 7a).

For soil fungi, AP was negatively correlated with the relative abundance of Calcarisporiellomycota, Glomeromycota, and Unclassified_k__Fungi. NH_4^+-N and SS had positive correlations with Mucoromycota, while NH_4^+-N, TN, SS, and SWC had negative correlations with Calcarisporiellomycota. Additionally, pH had a positive correlation with Kickxellomycota, and TN had a positive correlation with Zoopagomycota (Fig. 7b).
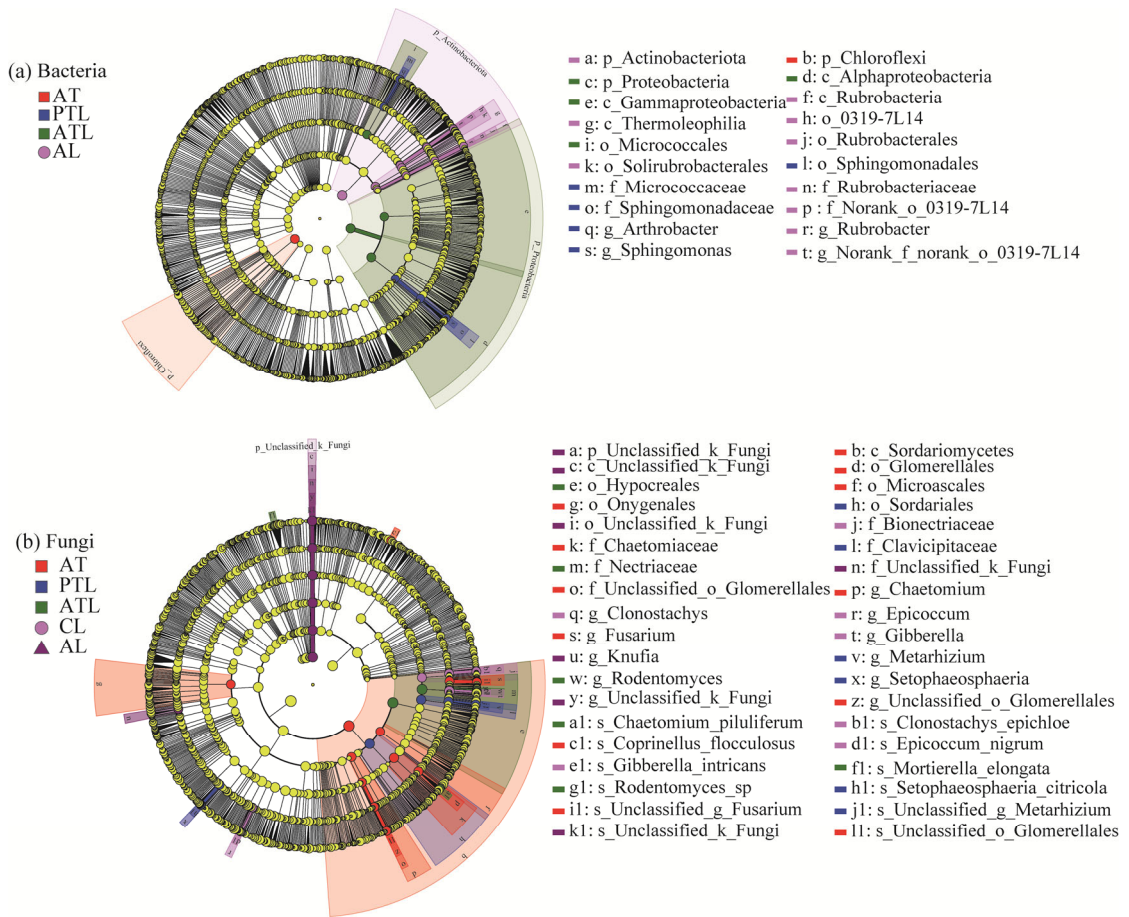
Fig. 5 Cladogram depicting the phylogenetic distribution of bacterial (a) and fungal (b) lineages among different land-use patterns. Linear discriminant analysis (LDA) score histogram was computed for species with varying abundances in bacterial and fungal communities, and identified using a threshold value of 4.0.
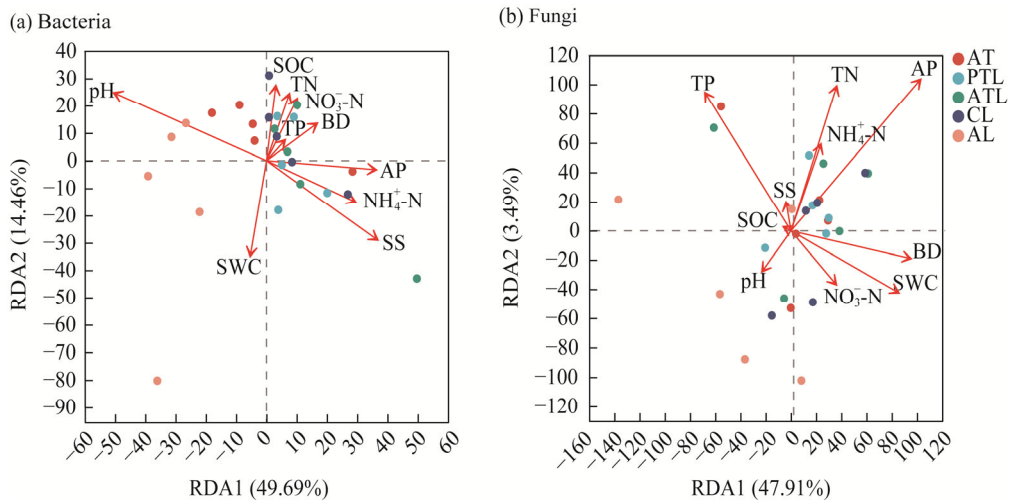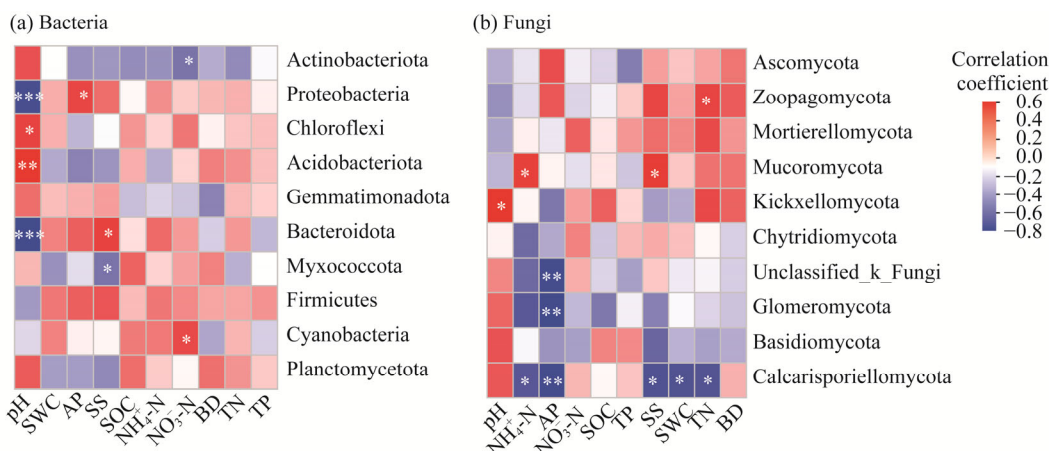

Fig. 6 Redundancy analysis (RDA) for the relationship between bacterial community and environmental variables (a), and between fungal community and environmental variables (b). SOC, soil organic content; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus; SS, soil salinity; SWC, soil water content, BD, bulk density. The abbreviations are the same as in Figure 7.

Table 3   Relationships between soil properties and two axes of redundancy analysis (RDA) for bacterial and fungal communities

Soil property	Bacteria				Fungi			
	RDA1	RDA2	R^2	P	RDA1	RDA2	R^2	P
SOC	0.1519	0.9884	0.128	0.203	−0.924	0.3824	0.000	0.998
TN	0.3703	0.9289	0.112	0.273	0.3729	0.9279	0.147	0.203
TP	0.7140	0.7002	0.015	0.780	−0.6587	0.7524	0.200	0.093
NH_4^+-N	0.9286	−0.3710	0.220	0.067	0.4054	0.9141	0.053	0.563
NO_3^--N	0.4953	0.8687	0.107	0.310	0.7562	−0.6544	0.038	0.649
AP	0.9982	−0.0603	0.282	0.028*	0.7652	0.6437	0.302	0.020*
pH	−0.9334	0.3588	0.654	0.010*	−0.6964	−0.7176	0.017	0.804
SS	0.8473	−0.5310	0.430	0.052	−0.2629	0.9648	0.005	0.949
SWC	−0.2024	−0.9793	0.213	0.081	0.9142	−0.4052	0.143	0.167
BD	0.8365	0.5480	0.089	0.305	0.9804	−0.1968	0.149	0.175

Note: *, $P<0.050$ level.

Fig. 7   Correlations between bacterial community and soil properties (a) and between fungal community and soil properties (b). *, $P<0.050$ level; **, $P<0.010$ level; ***, $P<0.001$ level.

4   Discussion

4.1   Variations of soil microbial richness and diversity

The conversion of farmland into forest land on a large scale in the Loess Plateau has resulted in changes to vegetation, soil properties, and soil microbial communities. Human-induced land-use patterns can lead to alterations in soil properties (Tian et al., 2017), thereby directly influencing the composition and diversity of soil microbial communities (Rodrigues et al., 2013; de Carvalho et al., 2016; Yang et al., 2019; Cao et al., 2021).

4.1.1   Soil microbial richness and alpha-diversity

Consistent with our hypothesis, significant disparities in the alpha-diversity of soil fungal communities were observed across various land-use patterns. A similar pattern was evident in the soil bacterial community, except for the Shannon index (Table 2). This result indicated that the impact of land-use conversion on soil fungal communities is more pronounced than that on bacterial communities, primarily due to the unique physiological characteristics of soil fungi such as aerial hyphae and spore reproduction (Roper et al., 2010), which give them greater anti-interference ability compared with bacterial communities. This finding contrasts with

previous studies examining the response of bacterial and fungal communities to land-use changes (Qin et al., 2021; Zhang et al., 2023). It is noteworthy that the response of soil bacterial alpha-diversity to land-use changes exhibited a slower rate compared with that of soil fungi, implying a higher resistance of bacteria towards interference in comparison with fungi. This phenomenon can be attributed to the relatively greater richness and diversity of bacteria as compared with fungi (Table 1), along with their capacity for metabolizing a broader range of compounds (Wang et al., 2019). These findings align with those reported by Uroz et al. (2016). The conversion of land-use had minimal impact on the richness or diversity (Shannon index) of soil bacterial communities, but exerted significant influence on fungal communities (Table 1).

4.1.2   Soil microbial beta-diversity

The beta-diversity of soil bacteria exhibited significant differences between AL and other land-use patterns (Fig. 3a), while that of soil fungi did not show any statistically significant difference (Fig. 3b). This finding contradicts Hypothesis 1, which could potentially be attributed to the heterogeneity of habitats (Sun et al., 2020). The intricate nature of root morphology and exudates in plant species across diverse land-use patterns can create diverse soil microbial habitats, thereby exerting profound influences on the composition and the structure of soil microorganisms (Pii et al., 2016). Land-use change modifies soil parameters like moisture, pH, and nutrient contents, which impacts the structure of soil microbial community (Zhou et al., 2020; Zhang et al., 2022). In this study, soil pH plays a pivotal role in determining the populations of soil bacterial (Table 3), as it exerts influence on microbial communities by modulating various enzyme activities, overall metabolism, nutrient availability, and mitigation of ionic toxicity within the soil (Zhalnina et al., 2015). AP exerts a substantial influence on the beta-diversity of both bacteria and fungi (Table 3), which may be due to its pivotal role in ribosomal RNA synthesis (Xu et al., 2020; Ren et al., 2021), similar to that of Yu et al. (2021).

4.2   Soil microbial composition

At the phylum level, the composition of soil bacteria (Fig. 4a) and fungi (Fig. 4c) in this study exhibited a resemblance to previously reported findings for the Loess Plateau by Tian et al. (2017), Yang et al. (2020a), and Zhang and Lv (2021). This finding supports the notion that habitats such as semi-arid areas like the Loess Plateau exert a predominant influence on shaping soil microbial communities (Tian et al., 2017). However, the distinct physiological response curves exhibited by individual microbial taxa, encompassing both specialist and generalist strategies in response to environmental changes such as land-use conversion, can result in variations in soil microbe composition across different land-use patterns (Lennon and Jones, 2011).

4.2.1   Bacterial community composition

Significant variations were observed in the bacterial communities across different land-use patterns, including Actinobacteriota, Proteobacteria, and Chloroflexi (Fig. 3c), thereby providing support for our Hypothesis 2. These findings imply that changes in land-use can have a substantial impact on the relative abundance of most bacteria within the study area. Consistent with findings of Yang et al. (2020a), who found that alterations in soil properties resulting from land-use patterns influence both the abundance and composition of soil microbial communities. Actinobacteriota, Proteobacteria, and Chloroflexi are the predominant bacterial phyla in the soil. Actinobacteriota and Chloroflexi are recognized as oligotrophic bacteria due to their ability to thrive in nutrient-limited environments. Moreover, Actinobacteriota is a gram-positive bacterium exhibiting denitrification capabilities and demonstrating robust metabolic capacity under conditions of low temperatures and limited water content (Johnson et al., 2007). The Proteobacteria, which are anaerobic bacteria, exhibit a wide distribution in vegetation areas due to the rapid growth and metabolic diversity. They possess significant phylogenetic, ecological, and pathogenic implications while being actively involved in energy metabolism (Bryant and Frigaard et al., 2006; Mukhopadhya et al., 2012). They encompass most of the nitrogen-fixing, ammonia-oxidizing, and denitrifying bacteria (Xiao and Veste, 2017), while also serving as an

indicator of soil nutrient status (Deng et al., 2018). The Actinobacteriota and Chloroflexi exhibited the highest relative abundances in AL (Fig. 3c). This observation can be attributed to the low natural nitrogen content of AL and land degradation (Table 1), as a significant negative correlation between Actinobacteriota and NO_3^--N was found in this study (Fig. 7a). Furthermore, it is worth noting that soil nutrient availability is influenced by pH (Javed et al., 2021). Actinobacteriota in soil may be influenced by multiple environmental factors (Qin et al., 2021). Moreover, Actinobacteria have been identified as the predominant bacterial phylum in grassland across varying degrees of degradation (Zhou et al., 2019). The disparity in the relative abundance of Chloroflexi could potentially be attributed to the elevated pH levels observed in AL (Table 1). This investigation has unveiled a significant positive correlation between Chloroflexi and pH (Fig. 7a), potentially because a high pH value alleviates soil nutrient limitations and exacerbates soil infertility, thereby indicating enhanced survival competitiveness in soils with lower organic matter content (Klatt et al., 2013). The pH values may also influence the relative abundance of Proteobacteria in AL. Our study revealed a significant inverse correlation between pH and Proteobacteria (Fig. 7a), which emerged as the second most predominant phylum among all soil samples. However, in comparison with AL, other land-use patterns (CL, ATL, PTL, and AT) exhibited a significantly higher relative abundance of Proteobacteria (Fig. 3c). This observation suggests that an elevated level of soil nutrients may lead to an increased relative abundance of Proteobacteria, which aligns with the findings reported by Zhang and Lv (2021). The diverse metabolic capabilities possessed by Proteobacteria could account for this phenomenon (Qin et al., 2021). Most of these populations exhibit co-trophic behavior, indicating their ability to thrive in environments with higher resource availability (Nelson and Carlson, 2012). Additionally, microbial communities can be categorized as copiotrophs or oligotrophs. Copiotrophs thrive in nutrient-rich environments, while oligotrophs possess a competitive advantage under conditions of low-resource stress (Fierer et al., 2007). Proteobacteria were identified as the predominant phylum in copiotrophic soils, whereas the ratio of Proteobacteria to Acidobacteria was found to serve as an indicator of SOC, with oligotrophic soils exhibiting lower ratios. The present study further reinforces this finding by demonstrating that the lowest ratios were observed in AL, while the highest ratios were found in other land-use patterns (CL, ATL, PTL, and AT). Therefore, it is plausible to suggest that conversion of land-use and soil properties are significant explanatory variables for bacterial community structure.

4.2.2   Fungal community composition

The fungal community in this study was predominantly composed of Ascomycota and Basidiomycota, which are known to thrive in cooler and drier environments due to their evolutionary history (Treseder et al., 2014). Specifically, Ascomycota plays a pivotal role in fungal communities under conditions of carbon or nutrient limitation as well as drought stress (Tedersoo et al., 2014; Clemmensen et al., 2015; Sterkenburg et al., 2015). The Loess Plateau is characterized by the prevalence of Ascomycota and Basidiomycota as the dominant fungal taxa (Zeng et al., 2020). Ascomycota consistently emerges as the predominant phylum in this area (Liu et al., 2019). Our current investigation reveals that lower AP contents in AL were associated with a decreased abundance of Ascomycota and an increased abundance of Basidiomycota compared with other land-use patterns with higher AP contents (Table 1; Fig. 7b). These findings are consistent with the results reported by Lauber et al. (2008), suggesting that disparities in AP among different land-use patterns may be the primary factor contributing to variations in populations of Ascomycota and Basidiomycota (Lauber et al., 2008). Furthermore, it has been observed that various species employ distinct life strategies to adapt to environmental changes (Huang et al., 2021). The members of Ascomycota predominantly exhibit saprophytic lifestyles and possess specialized enzymes for the decomposition of organic matter (Zeng et al., 2020). In contrast, Basidiomycota typically establishes symbiotic associations with root systems (Wubet et al., 2012). It is worth noting that the presence of Glomeromycota in the planted lands (CL, ATL, PTL, and AT) was almost negligible (Fig. 3b), indicating their adaptation to oligotrophic

conditions and nutrient-poor environments in AL. It should be noted that Glomeromycota has the ability to establish arbuscular mycorrhizal associations with terrestrial plants (Heděnec et al., 2020). Arbuscular mycorrhizal fungi derive nutrients from organic matter, thereby benefiting host plants, influencing decomposition processes, and modulating fungal communities in response to limited soil P availability rather than excessive P availability (Xu et al., 2018). These findings lend support to Hypothesis 2. The inter-species interactions contribute to the proportional redistribution of organisms within a shared habitat and environment (Huang et al., 2021). Importantly, the negative correlation observed between Ascomycota and Basidiomycota in soil nutrients indicates their occupancy of similar ecological niches, implying a competitive relationship for resource utilization (Huang et al., 2021).

4.3   Dominant factors driving the variation in soil microbe

According to RDA, soil pH exerts a dominant impact on the composition of soil bacterial communities at the phylum level, while soil AP primarily shapes the composition of soil fungal communities (Fig. 6; Table 3), which aligns with Hypothesis 3. These findings confirm the significant role of soil pH and AP in influencing the microbial community under different land-use patterns, which is supported by the Spearman correlation (Fig. 7). The findings of the study revealed that soil pH in the planted lands (CL, ATL, PTL, and AT) was comparatively lower than that of AL, thereby enhancing soil microbial activity and promoting the soil organic matter decomposition (Yang et al., 2020a). The responses of soil bacteria and fungi to pH in the study area exhibited distinct patterns. This disparity could be attributed to variations in soil pH influencing resource acquisition and utilization by soil bacterial communities (Cheng et al., 2021), consequently constraining the survival of specific groups such as Acidobacteriota and subsequently limiting microbial physiological activity (Zhou et al., 2020). The composition of fungal communities is primarily influenced by soil AP, in contrast to bacterial communities. This observation aligns with the findings reported by Lauber et al. (2008) and Tian et al. (2017), suggesting potential associations with distinct microhabitats corresponding to different land-use patterns or specific fungal functions (Tian et al., 2017). These results further underscore the differential responses of bacterial and fungal communities to various soil chemical properties.

According to the dominant factors driving the variation in soil microbial, inadequate land management practices in AL have led to an increase in pH value and a decrease in AP (Table 1). Consequently, the variety and composition of soil microbial communities have been greatly altered by these changes. Therefore, it is crucial to implement AL re-cultivation strategies aimed at restoring and preserving soil fertility and functionality.

5   Conclusions

The present study suggests that variations in land-use patterns have led to alterations in soil properties, subsequently influencing the diversity and structure of microbial community in the Loess Plateau, China. From both economic and ecological perspectives, the planted lands have more advantages compared with abandoned lands in the study area. However, given the relatively small scale and the fact that the samples were collected from a single site in the study, further investigations conducted in other regions of the Loess Plateau are imperative to establish a more widely applicable result.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

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